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# Roads may act as barriers to flying insects: species composition of bees and wasps differs on two sides of a large highway

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## Abstract

Roads may act as barriers to animal movements, but direct barrier effects on insects have rarely been studied. In this study we collected data on bees and wasps along two sides of a large road in Sweden using yellow pan traps. We then analyzed if the species composition differed between the two sides of the road; first for the whole community, and then only for the smallest species (which typically are poorer dispersers). As a complement, we analyzed if different vegetation variables differed between the two sides of the road, as this may also affect differences in species composition. Finally, we analyzed if species richness and abundance in general differed between the two sides and how these two response variables were explained by the vegetation variables. There was a significant difference in species composition between the eastern and the western side of the road when analyzing the whole community, and this relationship became even stronger when the largest species were excluded. The vegetation variables did not strongly differ between the two sides, and there was no difference in species richness and abundance of bees and wasps either. Abundance was, however, explained by the number of flowering plants in the surroundings of the trap. Even though using a rather limited data set, our results indicate that large roads may act as barriers on the movement of bees and wasps, especially for small species with poor dispersal ability. On the other hand, road verges may be important habitat for many species, which leads to a potential conflict that is important to consider in the planning of green infrastructure.

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**Keywords**
Infrastructure, barrier effects, habitat fragmentation, Aculeata, wild bees

## Introduction

The increasing amount of infrastructure and road networks in the landscape is a major cause of habitat fragmentation (e.g. Forman and Alexander 1998, Jackson and Fahrig 2011). Roads may act as barriers to animal movements, resulting in animals avoiding or not being able to cross roads, but also leading to animals suffering a high mortality when moving between habitats intersected by roads (Forman and Alexander 1998, Trombulak and Frissel 2000). Most studies on barrier effects of roads on animals have so far mainly focused on mammals, birds and amphibians (c.f. Trombulak and Frissel 2000). Considerably fewer studies have focused on insects (Muñoz et al. 2015), despite the fact that insects are the most diverse and species rich animal group on earth.

Some studies on the effects of roads on insects exist, indicating that large roads can cause disruption of movements between habitats in butterflies (Askling et al. 2006) and bumblebees (Bhattacharya et al. 2003). There is also some recent evidence that the mortality of insects can be substantially high along large roads (McKenna et al. 2001, Soluk et al. 2011, Skórka et al. 2013, Baxter-Gilbert et al. 2015, Skórka et al. 2015). Barrier effects may also ultimately have the consequence that populations on different sides of roads become genetically isolated (Keller and Largiader 2003). It is likely that barrier effects of roads are most pronounced in species with poor dispersal ability, and studies of butterflies indicate that it is mainly smaller species that avoid crossing roads (Askling et al. 2006) and also suffer from the highest road mortality (Skórka et al. 2013). There is thus a possibility that roads can affect the community composition of insects, particularly with respect to species that are poor dispersers. However, to our knowledge this has not been investigated before.

One additional reason that barrier effects of roads on insects deserve attention is that road verges have been highlighted as important habitat for many species (Way 1977), and may as such be considered for conservation actions. In Sweden and many other parts of Europe, changes in land use have caused dramatic areal declines in grassland and meadow habitats during the last century (Critchley et al. 2004, Cousins 2009), and road verges may today be important surrogates of these grasslands in modified landscapes (Ruiz-Capillas et al. 2013). Road verges can be species rich in vascular plants (e.g. Way 1977) and may therefore function as habitats for pollinating insects (Saarinen et al. 2005, Hopwood 2008). Furthermore, roads can also serve as linear elements in the landscape, thereby facilitating dispersal of insects alongside the roads (Sjödin et al. 2008). However, if roads act as barriers and obstruct dispersal between habitats on different sides of roads for insects inhabiting the road verges, there is a potential conflict between the conservation value of the road verges and a fragmentation effect from the road (Skórka et al. 2013).

Aculeata (i.e. bees and wasps) is a species rich group that may provide several ecosystem services (e.g. Harris 1994, Tscharntke et al. 1998). Especially bees, but also to some extent wasps, are flower-visiting insects important for pollination of crops and native plants (Tscharntke et al. 1998). Wasps are also predatory insects, potentially reducing populations of pest insects (Harris 1994). Moreover, these insects have been proposed as important bioindicators for ecological change and habitat quality (Tscharntke et al. 1998). It is known that many bees and wasps utilize road verges for foraging and nesting (Hopwood 2008, Hanley and Wilkins 2015), but very little is known about how large roads may act as barriers to movements between habitats and thereby affecting community composition.

The aim of this study was to investigate if large roads may act as barriers on the movements of bees and wasps (Aculeata). Specifically, we compared the species composition of bees and wasps on different sides of a large road, both for the whole community and for only the smallest species. We expected the community composition to differ between the two sides, given that there was a barrier effect. As a complement, we also analyzed general differences in foraging and nesting variables, and the abundance and number of species of bees and wasps, between the two sides of the road.

## Methods

### Field inventory

We performed an inventory of bees and wasps (Aculeata) using yellow pan traps at five sites in Sollentuna municipality, north of Stockholm, during late July-early August 2015. The sites were situated along the highway E4, which runs approximately in a north-south direction through Sollentuna municipality (Figure 1). This segment of E4 highway has a maximum speeding limit of 100 km/h and has a traffic flow of approximately 90 000 vehicles/day. We selected the sites as to be more or less evenly distributed along the highway. However, exact sampling locations had to be determined in the field after considering logistic factors, as large parts of the highway were not always easily accessible. At the sites, the distance from the road to the vegetation was approximately 50 cm, separated by a stripe of gravel.

At each site, we placed four yellow pan traps, two on each side of the road, i.e. 20 traps in total. At four sites the distance between the traps across the road was approximately 50 m and at one site the distance was approximately 200 m. The distance between traps at the same side of the road varied somewhat between the sites, but the distance between the traps on the same side of the road were at each site approximately the same as the distance to the nearest trap on the opposite side of the road (with a square-shaped setup, were each trap was a corner). The vegetation at the sites had previously been mowed during the summer. The exact dates for mowing are not known, but the vegetation height was between 15–40 cm at the sites.

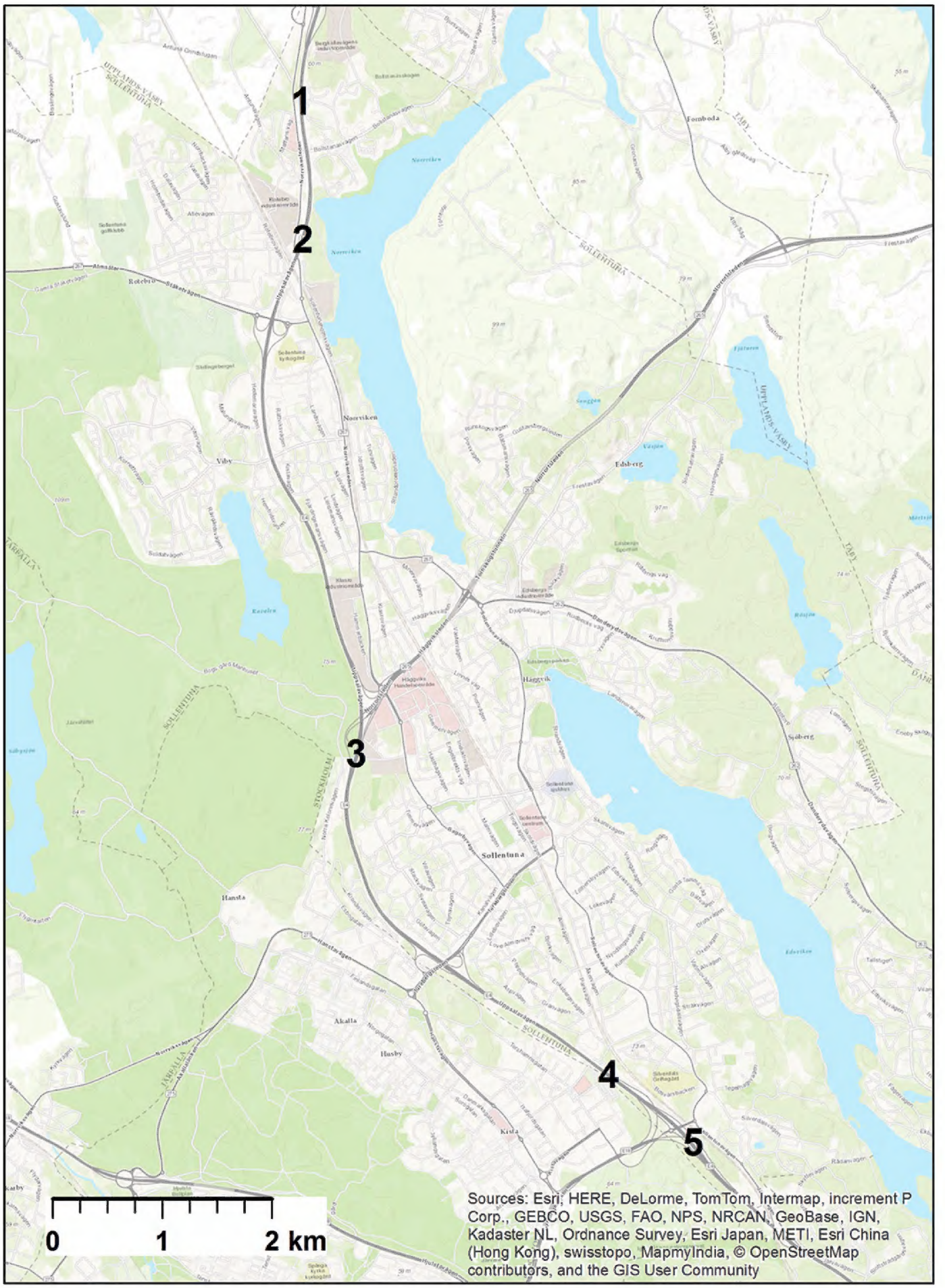


**Figure 1.** Overview of the study area along the E4 in Sollentuna, showing the five sites where communities of bees and wasps were sampled with two traps on each side of the road.

The traps consisted of 0.8 l aluminum boxes (with the lid removed) sprayed with yellow paint. The traps were filled with water and a drop of detergent with the purpose to reduce surface tension of the water surface. The traps were placed at the sites during

early morning at days with suitable weather conditions (sunny weather, 20–25°C), and the traps were emptied and removed from the sites four days later, at late afternoon/evening. The collected material was stored in ethanol. All bees and wasps where identified to species-level.

At each collection plot (i.e. four plots per site), we made a rough estimation of three variables of importance for foraging and nesting of bees and wasps. These variables were based on four photographs of the vegetation in a 1x1 m wooden frame on the ground placed at four different positions at each collection plot; one at the position of the trap, two positions ten meters from the trap in each direction parallel to the road, and one position ten meters from the trap perpendicular to the road. These photographs where then used to estimate three variables: 1) the number of flowering plant species within the test square (as a qualitative measure of the foraging habitat), 2) the proportion of vegetation (in %) covered by flowering plants within the test square (as a quantitative measure of foraging habitat), and 3) the proportion of the area (in %) covered by bare soil within the test square (as a measure of nesting habitat availability). Based on the estimations from the four photographs, we then calculated an average of the three variables for each collection plot, which was used in the analysis. At each site we also subjectively assessed the inclination of the road verges on the eastern and western side of the road based on photographs taken at each plot. This was done to detect possible patterns in inclination between the two sides of the road that potentially could affect our results.

**Statistical analyses**

To test whether the species composition of the bee and wasp community differed between the eastern and the western side of the E4 highway, we used Canonical Correspondence Analysis (CCA; Oksanen et al. 2015). Trap catches for traps placed on the same side of the road at each site were pooled, as these trap catches may not be regarded as independent replicates. First, we performed a CCA on the entire community of bee and wasp species. We included two explanatory variables, (1) side of the E4 (eastern/western) to test for the barrier effect of the road and (2) the north coordinate to control for any potential north-south gradient in the data. Second, we performed a CCA only on the smallest species, as they could be expected to have a lower dispersal ability compared to the larger species (e.g. Greenleaf et al. 2007), and thus may be more sensitive to barrier effects. For this purpose, we categorized all species as either small or large. We used the size of a honeybee *Apis mellifera* as the criterion for a large species following Samnegård et al. (2015), as this species usually is considered as being mobile with a relatively high dispersal capacity (Schneider and Hall 1997; Beekman and Ratnieks 2000). We categorized all species larger than the honeybee, which has a maximum body length of approximately 16 mm (Amiet and Krebs 2014), as being large (mobile, 9 species), and all other species as being small (less mobile, 30 species) and performed a CCA on only the small species, with side of E4 (eastern/western) and

the north coordinate as the explanatory variables. The data on size of the species were collected from identification literature and reference collections (See Suppl. material 1: S1 Aculeata species list and body lengths), and we consistently used the maximum body length reported.

As a complementary analysis, we investigated if the road verges on both sides of the E4 differed in vegetation characteristics, as these variables may have consequences for the interpretation of the results from the CCAs. For this purpose, we analyzed the number of flowering plant species, cover of flowering plants (in %), and cover of bare soil (in %) with the side of E4 (eastern/western) as the explanatory variable, using generalized linear mixed models (GLMMs) with site as a random factor.

Furthermore, we also examined if there were any general differences in abundance and number of species in bees and wasps between the eastern and the western side of the E4, and if the three vegetation variables could explain these two response variables. For this purpose, we used GLMMs with Poisson distributions and site identity as a random factor. However, initial analyses indicated that the number of flowering plant species was tightly correlated with the cover of flowering plants (Pearson correlation: $r=0.73$, $p<0.001$), and as the first provided a slightly better model fit (when tested separately) we decided to only include the number of flowering species, the cover of bare soil and the side of the road as explanatory variables in the final models.

All analyses were performed using R 3.2.2 (R Development Core Team 2015) with add-on libraries VEGAN (version 2.3-2) for the CCAs and glmmADMB for the GLMMs.

## Results

In total, 111 individuals of 39 species of bees and wasps (Aculeata) were collected in the 20 yellow pan traps. The trap catch comprised 20 bee species (Apoidea), while the remainder consisted of various wasp species, such as Crabronidae (8 species), Pompilidae (6 species), Sphecidae (3 species), Tiphidae (1 species) and Vespidae (1 species) (see Suppl. material 1). We found several relatively rare species such as *Lestica clypeata, Panurgus calcaratus* and *Psenulus brevitarsis,* of which the first two previously were red-listed in Sweden (Gärdenfors 2005, Gärdenfors 2010). *Panurgus calcaratus* and *Philanthus triangulum* have been suggested to be indicators for species rich sandy habitats and dry meadows in Sweden (Swedish Board of Agriculture 2003, Karlsson 2008).

The canonical correspondence analyses (CCAs) showed a significant difference in species composition between the eastern and the western side of E4 (Table 1, Figure 2) when analyzing the whole community, and this pattern became even stronger (lower p-value) when we excluded the largest species (i.e. with a maximum body size >16 mm) (Table 1, Figure 2). In both analyses, there were also significant relationships between the species composition and the north-south gradient (Table 1). The variation explained by the two explanatory variables was 37% for the whole community and 47% when excluding the largest species.

**Table 1.** Results from tests of the explanatory variables in the CCA-models with all species included and with the largest species (>16 mm in maximum body length) excluded.

| Explanatory variable | All species | | Large species excluded | |
|---|---|---|---|---|
| | F | p-value | F | p-value |
| East/West | 2.04 | 0.021 | 2.60 | 0.003 |
| North coordinate | 2.12 | 0.016 | 2.75 | 0.005 |

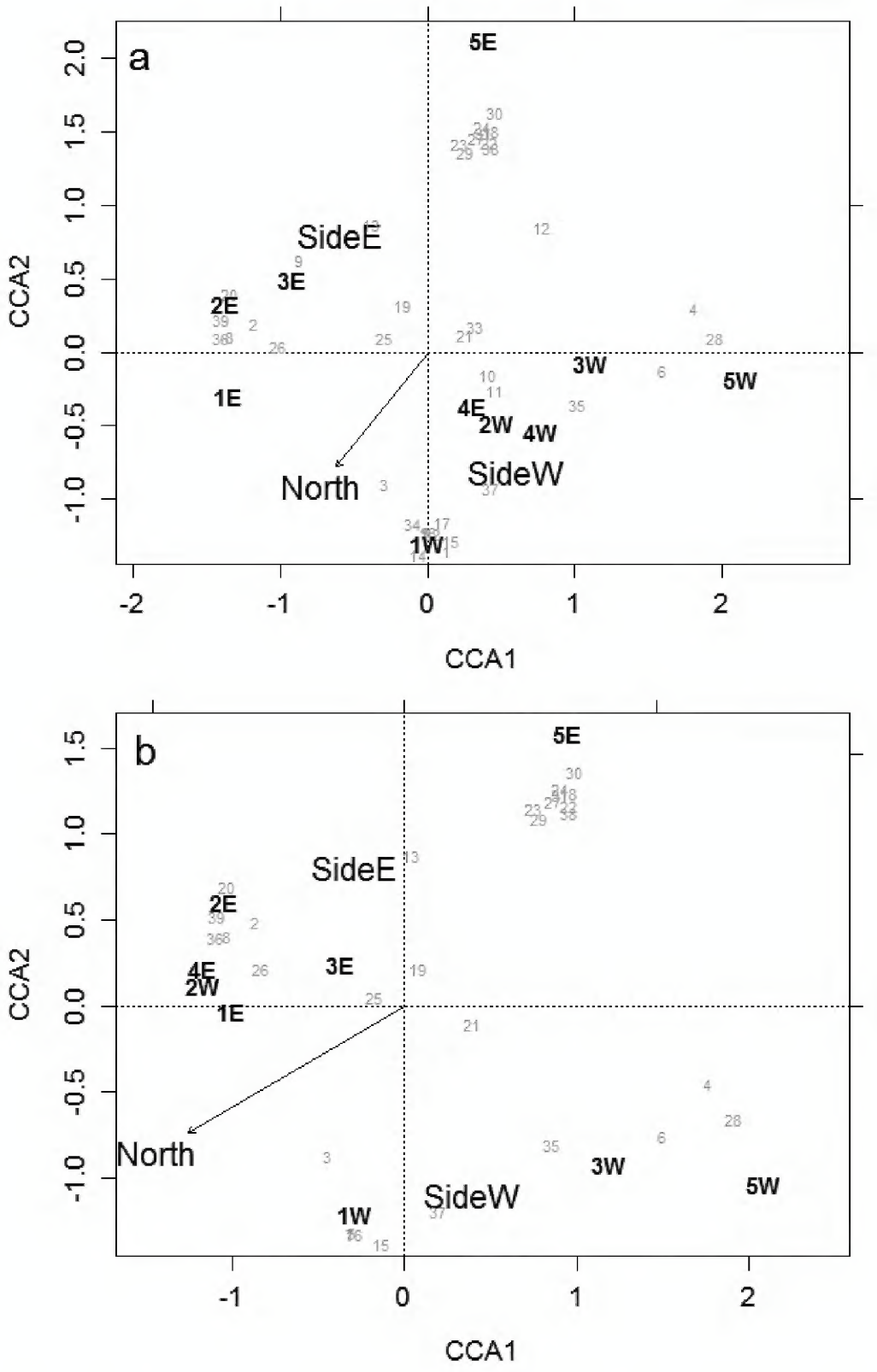


**Figure 2.** Ordination plots for communities of bees and wasps along the E4 in Sollentuna, where **a** shows the result for the analysis of the whole community and **b** the result for the analysis where the large species (>16 mm) were excluded. Grey small numbers refer to different species (Suppl. material 1) and black larger text shows the sites and the two explanatory variables (eastern or western side of the road, and the north-south gradient). To improve visualization the species are plotted with a small scatter.

**Table 2.** The abundance and number of species of bees and wasps (Aculaeta) in relation to the side of the road, number of flowering plants and the cover of bare soil based on generalized linear mixed models (Poisson error distribution).

| Explanatory variable | Abundance | | Number of species | |
|---|---|---|---|---|
| | Estimate (SE) | p-value | Estimate (SE) | p-value |
| Side of the road | -0.17 (0.22) | 0.44 | -0.33 (0.25) | 0.18 |
| Number of flowering plant species | 0.30 (0.13) | 0.02 | 0.25 (0.14) | 0.08 |
| Cover of bare soil (%) | -0.22 (0.14) | 0.12 | -0.21 (0.16) | 0.19 |

We found no significant difference in the number of flowering plants ($p = 0.10$), the cover of flowering plants ($p = 0.16$), or the cover of bare soil ($p = 0.81$) between the two sides of the E4. The abundance and number of species of bees and wasps did not differ significantly between the two sides either (Table 2). However, the abundance of bees and wasps increased significantly with an increasing number of flowering plant species, while the number of bee and wasp species did not show such a relationship (Table 2). The cover of bare soil did not explain any of the two response variables. There was no clear pattern in the inclination of the road verges between the eastern and western side of the road: at site 1 both verges were inclining rather strongly towards the road; at site 2 the eastern road verge was flat while the western road verge inclined weakly towards the road; at site 3 both verges inclined weakly from the road; at site 4 the eastern road verge inclined towards the road while the western inclined from the road; and at site 5 both verges were rather flat.

## Discussion

By analyzing differences in species composition along two sides of a large road we found indications that roads may act as barriers on the movement of bees and wasps. Even if the yellow pan traps were in most cases only separated with ~50 m across the road, the two analyses of the community composition both pointed in the same direction – the community composition differed between the western and eastern side of the road. Also when considering the fact that the trap catches where rather small (~10 individuals/site), the results show that species composition at sites situated on the same side of the highway were more similar to each other compared to the sites at the opposite side (Figure 2). There were also differences in species composition in the north-south direction, which is more expected as this gradient spanned almost 9.5 km. The barrier effect seemed stronger when excluding the large species from the community (based on the lower p-value and the increased explained variation). We suggest this pattern to be a result of the fact that for flying insects large species in general have a higher mobility, thereby constituting better dispersers than small species (Gathmann and Tscharntke 2002, Greenleaf et al. 2007). This suggests that larger species do not

perceive large roads as barriers as much as smaller species. For example, among the large species in this study almost 45% are bumblebees, which are known to be strong fliers with the ability of quickly covering long distances (Walther-Hellwig and Frankl 2000, Steffan-Dewenter et al. 2001, Hagen et al. 2011) and possibly also flying relatively high above the ground compared to the smaller species. Even though we did not directly study insect movements and mortality, our results agree with previous studies on insects (Askling et al. 2006, Skórka et al. 2013). Askling et al. (2006) showed that smaller butterfly species (*Aphantopus hyperantus* and *Maniola jurtina*) were less likely to move between pastures on different sides of a large road compared to larger species (*Pieris rapae*, *Gonepteryx rhamni* and *Anthocharis cardamines*). The suggested reason for this was that the first two species have lower dispersal abilities and often tend to fly close to the ground, while the latter three species often move at higher levels above ground and are capable of quickly covering great distances across a landscape (Askling et al. 2006). Flying close to the ground also increases the susceptibility to motor vehicles (Soluk et al. 2011), which may explain why small butterfly species have been shown to be overrepresented among road-killed butterflies (Skórka et al. 2013). We are currently not able to determine whether our results are best explained by an increased mortality in smaller species, or if smaller species to a greater extent avoid crossing large roads or highways. To investigate this would require a study design with several roads, preferably of the same width, along a gradient in traffic volume (McKenna et al. 2001). However, even though we did not analyze the actual mechanism, our result suggests that large roads could have a fragmentation effect in the landscape by acting as barriers to insects, with consequences for community compositions that is critical enough to justify detailed research.

Road verges have been highlighted as important grassland habitats, often rich in species of vascular plants and pollinators (Way 1977, Saarinen et al. 2005). Moreover, these habitats are often important for red-listed and rare species (Helldin et al. 2015). This was also confirmed by this study, where some rare or interesting species from a conservation perspective were found. However, the number of flowering plant species along the road verges had a relatively weak effect on the richness and abundance of bees and wasps, and only for abundance the relationship was statistically significant. Somewhat surprising, we found no effect of the cover of bare soil, which may indicate that the soil along the road verges is not optimal as nesting habitat for these species. However, it may also be due to the method used to quantify this variable. The occurrence of bare soil has a rather patchy distribution along roads, and it may therefore be more difficult to get a representative quantification of this variable based on four 1x1 m squares compared to e.g. the cover of flowers which usually is more evenly distributed. There was no clear pattern in the inclination of the road verges between the eastern and western side of the road, and it is therefore unlikely that the differences in community composition we found was caused by differences in inclination. However, inclination can most likely affect the microclimate of the road verges and it would therefore be interesting to investigate its effect on insect communities in future studies.

## Conclusions and implications for conservation

Even though using a rather limited data set, our results indicate that large roads may act as barriers to bees and wasps, especially for small species with poor dispersal ability. This means that large roads potentially can affect the ecosystem services these species provide (Baxter-Gilbert et al. 2015), such as pollination and biological control (e.g. Harris 1994, Tscharntke et al. 1998). On the other hand, road verges may constitute important habitat for many insects (Saarinen et al. 2005, Hopwood 2008), which leads to a potential conflict between the conservation value of the road verges and a fragmentation effect from the road. The severity of this conflict may, however, depend on several factors, such as traffic volume, the quality and management of the road verges, and the proportion of grasslands in the surrounding landscape (Skórka et al. 2015). All this is something that should be taken under consideration when developing green infrastructure, which is currently being pointed out as an important step towards the success of the EU 2020 Biodiversity Strategy (European Commission 2016). Examples of conservation measures to decrease fragmentation effects of large roads may be bridges with vegetation, similar to wildlife crossings (Bissonette and Cramer 2008), or tunnels, where bees and wasps (and other organisms) can move across or under the road. In our study, such movements could also be the reason for the similarity between the western and eastern communities at site two (Figure 2), because relatively close to this site there is a potential crossing under the road. However, this is something that needs further investigation. In general, we believe that more research is needed within the area of roads as barriers to insect communities, and the effectiveness of different conservation measures to decrease the negative impact of roads in the landscape.

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## Supplementary material 1

**Species list and body lengths of the 39 *Aculeata* species**

Authors: Petter Andersson, Anna Koffman, N. Erik Sjödin, Victor Johansson

Data type: species data

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